



Mechanisms of Waterlogging Tolerance in Maize

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Maize (*Zea mays* L.) is one of the main sources of cereals for food, forage and processed industrial products. World production of maize is around 790 million tones and it serves as a staple food providing more than one-third of the calories and proteins in some countries. Maize is predicted to become the crop with the greatest production globally and demand for maize will double in the future world, by 2025. Waterlogging is one of the most hazardous natural occurrences for maize production and productivity in tropical and subtropical regions around the world. In South-East Asia, 15 % of all maize growing areas are affected by waterlogging problems, causing losses in maize production of 25–30 % almost every year. In India, heavy spring rainfall over a short period can lead to form the waterlogged soils for an extended period and cause severe damage to maize seedlings. The main cause of damage under waterlogging is respiration by plant roots, soil micro-flora and fauna leads to a rapid exhaustion of soil oxygen, resulting in hypoxia followed by anoxia, oxygen deprivation, which affect nutrient and water uptake, so the plants start wilting when surrounded by excess of water. Hence, the development of waterlogging-tolerant varieties with greater adaptation to waterlogging are essential to increase maize productivity in waterlogged soil and it should be one of the main aims of many maize breeders.

Introduction

Maize (*Zea mays* L.) is one of the most important cereal grains grown worldwide in a wider range of environments because of its greater adaptability. It has become a staple food in many parts of the world, with the total production of maize surpassing that of wheat or rice. With the development of DNA markers, quantitative trait locus (QTL) mapping methodologies, marker assisted selection (MAS), fine mapping and many genes responsible for water logging tolerance are identified, it makes easy for the researcher to concentrate on modification or use of those genes to develop new waterlogging tolerant crop varieties. QTL analyses of waterlogging tolerance have been studied in maize. Earlier studies reported that the early stage of maize development is the most sensitive stage during waterlogging period due to the growing point is below the soil surface, especially from the second to the seventh leaf stage. Recently, several QTL mapping studies of waterlogging tolerance have been reported in maize and its wild relatives, *Z. luxurians* and *Z. nicaraguensis*. A larger number of QTL for waterlogging tolerance-related traits have been identified during the maize seedling stage, such as root and shoot development-associated traits, capacity for tolerance to toxins, root aerenchyma formation, adventitious root formation, under reducing soil conditions and leaf injury. It has been reported that some maizelines can express adventitious (nodal) root formation (ARF) during flooding (Jatet *et al.*, 1975; Lizasoet *et al.*, 2001). In a study of ARF in teosinte, it was reported that *Z. luxurians* and *Z. mays* ssp. *huehue-tenangensis* exhibit a higher capacity for ARF than some maize inbreds (Mano *et al.*, 2005).

Genetic Mechanism of Waterlogging Tolerance

Waterlogging is an important abiotic stress constraint that causes significant yield losses in low-layingrainfed areas. Lack of oxygen supply triggers the adverse effects of waterlogging on plant growth, which hampers nutrient and water uptake, as a reason the plant starts to decompose. Usually this occurs from the tips of roots, and this causes roots to appear as if they have been pruned. The consequence is the plant's growth and development is stalled. Plants which can withstand waterlogging condition have mechanisms such as aerenchyma formation, adventitious root formation, increased availability of soluble sugar greater activity of glycolytic pathway and fermentation enzymes, and involvement of antioxidant defense mechanism to cope with the oxidative stress induced by waterlogging. Ethylene plays an important role in change of mechanisms of plants in deficiency of oxygen. It was also reported that ethylene induces the genes of enzymes associated with aerenchyma formation, glycolysis and fermentation pathway.

Role of Ethylene in Aerenchyma Formation: Root aerenchyma formation is considered to be one of the most factors for adapting to water logging stress condition. Root growth into hypoxic or anoxic waterlogged soil relies on internal aeration in plants. The plant hormone ethylene helps adapt to waterlogging by inducing the formation of aerenchyma, which is one of many adaptive features of plants at submergence to avoid anaerobiosis by increasing the availability of oxygen and provides a low-resistance pathway for the transport of oxygen from the shoot to the root apex. Waterlogging-susceptible crops including maize start to form aerenchyma after suffering waterlogging stress. Abiko *et al.* (2012) in a study for comparison of the formation of aerenchyma and radial oxygen loss barrier induction in roots of *Z.nicaraguensis* with roots of maize (inbred line Mi29), in a pot soil system and in hydroponics found growth of maize was more adversely affected by low oxygen in the root zone compared with *Z.nicaraguensis*. The role of ethylene accumulated can mediate many adaptive characteristics, such as adventitious root and aerenchyma formation to avoid oxygen deficiency under flooded conditions (Hu *et al.*, 2016). Maize (*Zea mays*) develops aerenchyma only under oxygen-deficient conditions and ethylene is involved in lysigenous aerenchyma formation (Yamauchi *et al.* 2016).

Role of Ethylene Accumulation in Adventitious Roots Formation: Accumulation of ethylene is very important for the induction of several responses of plants to flooding. However, little is known about the role of this gas in the formation of flooding-induced adventitious roots. Accumulation of ethylene in plants is responsible for adaptive plant responses to flooding. Ethylene plays an important role in shoot elongation in wetland plants, enabling a totally submerged plant to reach the water surface. During flooding adventitious roots facilitate gas transport and water and nutrient uptake, help take up nutrients and ensure plant survival (Sauter, 2013). Drew *et al.* (1979) suggested that endogenous ethylene may be stimulated the adventitious rooting and cortical air space formation in nodal roots in *Zea mays* by enhanced concentrations of arising either from entrapment of the gas by unstirred water layers around the roots and/or by increased biosynthesis.

Ethylene Production and Flooding: The compartmentalization of enzymes involved in ethylene synthesis plays an important role in a plant's response to flooding. Reaction is blocked in the aerobic root system.

Molecular Approaches for Waterlogging Tolerance

Accelerated synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC) takes place in roots following the induction of ACC synthase genes by hypoxia. Ethylene diffusion rate from root to water is 10 times slower than in air and, ethylene synthesis is increased in the hypoxic root system and in the aerobic shoot. Ethylene may be released to the internal channels of aerenchyma and then diffused to the root area. Synthesis is occurred in roots where high

amount of ACC (1-amino cyclopropane-1-carboxylic acid) is present, which is a precursor of ethylene. In recent years, significant progress has been made in the use of molecular approaches, viz., Marker Assisted Selection, identification of QTL (Quantitative Trait Loci), for plant breeding and it becomes easy for the researcher to develop new waterlogging tolerant crop varieties like maize and other crops.

Fine gene mapping: AnjoseSilva *et al.* (2007) carried out an experiment to determine inheritance of tolerance based on plant and root dry matter of young maize plants suggested that the tolerance to flooding is controlled by many genes according to the frequency distribution of F₂. Du *et al.* (2017) performed Bulk segregant RNA-seq (BSR-seq) to identify differentially expressed genes and Single Nucleotide Polymorphism (SNPs) associated with waterlogging tolerance and identified 18 overlapping SNPs with genomic positions mapped. Yu *et al.* (2018) identified a total of 110 trait-single nucleotide polymorphism associations spanning 16 genomic regions, single associations explained 2.88–10.67% of the phenotypic variance and detected favourable alleles of a key candidate gene (GRMZM2G110141), strongly suggesting that GRMZM2G110141 is a key waterlogging tolerance gene which enhanced waterlogging tolerance in segregating populations. Salah *et al.* (2019) carried out an experiment to determine the differences in morphological and physiological responses of maize to drought and excess soil water. According to their study SuperOxide Dismutase (SOD), activity of Peroxidase (POD), Ascorbate Peroxidase (APX), and Glutathione Reductase (GR) were the most important antioxidant enzymes under waterlogging, while Catalase (CAT) activity and Peroxidase (POD) distinctly seemed to play key role under drought stress. Panozzo *et al.* (2019) in a study on Morphological Changes and Expressions of *AOX1A*, *CYP81D8*, and Putative *PFP* Genes in a Large Set of Commercial Maize Hybrids Under Extreme Waterlogging reported *AOX1A* turned out to be the most informative gene in explaining morphological responses across hybrids (by discriminant analysis), up-regulation of *CYP81D1* and down-regulation of *PFP* should also be considered for preserving root growth, which showed the greatest impairment by waterlogging.

Conclusion

The regulation of plant growth and development processes under waterlogging stress is very complex, with different crops, different varieties of the same crop, and different growth periods of the same crop often showing great differences, while different plant species evolved different adaptation strategies. At present, research on crop waterlogging tolerance is mainly carried out from the perspective of morphological, structural, physiological, biochemical, and metabolic gene signal regulation. The most effective ways to enhance plant waterlogging tolerance will be (1) improving cultivation management to reduce the direct damage to crops caused by waterlogging and (2) using modern molecular biology technology to discover the key genes regulating waterlogging tolerance and verify their functions.

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